

# Genetic dissection of fruit quality components in melon (*Cucumis melo* L.) using a RIL population derived from exotic × elite US Western Shipping germplasm

Miriam K. Paris · Juan E. Zalapa · James D. McCreight · Jack E. Staub

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**Abstract** Growing environment dramatically influences melon (*Cucumis melo* L.;  $2n = 2x = 24$ ) fruit development and quality. Consequently, the characterization of quantitative trait loci (QTL) controlling melon fruit quality for application in marker-assisted selection (MAS) requires an assessment of genotype by environmental interactions, trait correlations, and QTL efficacy. Therefore, fruit quality traits [soluble solids content (SSC), mesocarp pressure (MP), fruit diameter (mesocarp + exocarp; FD), seed cavity diameter (endocarp; SCD), seed cavity to FD ratio (C:D), fruit shape (FS), and percentage of exocarp netting (PN) at time of harvest] were examined in 81 recombinant inbred lines (RIL) at two growing locations (California, and Wisconsin, USA) to identify the map position and consistency of QTL for MAS in a Group Cantalupensis U.S. Western Shipping market type background. RIL developed from a cross between U.S. Department of

Agriculture line USDA-846-1 and ‘Top Mark’ were used to identify 57 QTL in both location tested (SSC = 10, MP = 8, FD = 6, SCD = 9, C:D = 8, PN = 6, and FS = 10). The QTL were distributed across 12 linkage groups and explained a significant portion of the associated phenotypic variation ( $R^2 = 4\text{--}29\%$ ). Twelve of such QTL were consistently identified in the two locations tested [SSC (*ssc7.4* and *ssc10.8*), MP (*mp7.2*, *mp10.3*, and *mplg7.5*), SCD (*scd1.1*, *scd5.4*, and *scd8.5*), C:D (*cd2.1*), and PN (*pn2.1*), FS (*fs1.1* and *fs2.3*)]. The map positions of 18 QTL (FS = 7, SSC = 6, C:D = 3, SCD = 1, and PN = 1) were in equivalent (i.e., collinear) genomic regions with previous studies in Group Inodorus-based maps. Six of the collinear QTL were detected in both locations in our study (*ssc7.4*, *ssc10.8*, *fs1.1*, *fs2.3*, *pn2.1*, and *scd5.4*). The collinearity of these QTL with those identified in other maps, and their consistency across diverse growing environments portends their broad applicability in melon MAS.

Miriam K. Paris, Juan E. Zalapa contributed equally to the work described in this manuscript.

M. K. Paris · J. E. Zalapa (✉) · J. E. Staub  
USDA/ARS, Vegetable Crops Unit, Department of Horticulture, University of Wisconsin, 1575 Linden Dr., Madison, WI 53706, USA  
e-mail: jezalapa@wisc.edu

J. D. McCreight  
U. S. Department of Agriculture, Agricultural Research Service, Agricultural Research Station, 1636 East Alisal, Salinas, CA 93905, USA

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## Abbreviations

BLUPs Best linear unbiased predictions  
BLUEs Best linear unbiased estimations  
FD Fruit diameter

FS	Fruit shape
MP	Mesocarp pressure
PN	Percent netting at full-slip
C:D	SCD:FD ratio
SCD	Seed cell diameter
SSC	Soluble solids content

## Introduction

Melon (*Cucumis melo* L.;  $2n = 2x = 24$ ) is an economically important, cross-pollinated, vegetable species of the Cucurbitaceae family that possesses substantial morphological variation (Stepansky et al. 1999). This variation determines horticultural market class designations that include differences in mature fruit vary in shape, sweetness, color, SSC, exocarp characteristics, diameter, and weight (Silberstein et al. 2003; Monforte et al. 2004).

Genetic analysis of melon has led to the description of roughly 200 major genes that control morphological traits (Pitrat 2002). However, sparingly few of these genes have been assigned to linkage groups. Economically important genes that have been mapped include those for disease resistance (e.g., *Fom-1&2*, *Nsv*, *Pm*, *Pvr*, *CMV*, and *Vat*), flowering characters (e.g., *a* and *ms*), plant architecture (e.g., *si* and *lmi*), and ethylene production during fruit saturation (Dogimont et al. 2000; Perin et al. 2002b; Perchepey et al. 2005a, b). More recently, the map positions of complex traits contributing to fruit quality (Perin et al. 2002a; Monforte et al. 2004; Eduardo et al. 2007; Obando et al. 2008) and yield (Zalapa et al. 2007) controlled by quantitative trait loci (QTL) have been determined.

The identification and mapping of yield and quality QTL, however, has been hindered by a paucity of markers and the use of populations (i.e.,  $F_2$  and  $BC_1$ ) that are not uniquely suited for complex trait analysis (Baudracco-Arnas and Pitrat 1996; Wang et al. 1997; Oliver et al. 2001; Danin-Poleg et al. 2002; Silberstein et al. 2003). More recently, genetic maps have been developed from populations such as recombinant inbred lines (RIL; Perin et al. 2002a, b, c; Zalapa et al. 2007) and double haploid lines (DHL; Gonzalo et al. 2005) that allow for comparatively precise estimations of genetic effects (Beavis 1998). The concurrent development and use

of simple sequence repeat (SSR) markers for map construction in melon affords an opportunity for the development of a melon consensus map through map merging, and parallel determination of collinearity among maps originating from diverse parentage (Katzir et al. 1996; Danin-Poleg et al. 2000).

Fruit quality is critical to varietal marketability, and consists of a complex array of external [e.g., shape, exocarp features (netting, ribbing, sutures)] and internal (e.g., seed cavity size, sugar concentration, MP) characteristics. The inheritance of some FS and exocarp features (Kubicki 1962; Lippert and Legg 1972) and internal quality components (i.e., soluble solids, seed cavity; Lippert and Hall 1982; Kalb and Davis 1984) has been determined to allow for the development of improved, high quality commercial varieties.

Several FS and internal quality (fruit weight and shape, sugar content and flesh color) traits have been mapped employing progeny derived from a relatively wide cross (Group Inodorus  $\times$  PI 161375, Korea; Perin et al. 2002a; Monforte et al. 2004; Eduardo et al. 2007; Obando et al. 2008). Recently, the inheritance of yield components was determined using cross-progeny originating from a relatively wide cross (Group Cantalupensis  $\times$  unadapted exotic; Zalapa et al. 2006; Zalapa 2005). Yield-related QTL were subsequently mapped using RIL developed from these progeny (Zalapa et al. 2007). Since this RIL mapping population is dramatically different from that used by Monforte et al. (2004; Group Inodorus versus Group Cantalupensis), and has potential for increasing yield in commercial U.S. Western Shipping market class melon, a study was designed to map QTL associated with fruit quality using these RIL. The marker-trait associations so identified could be used in marker-assisted selection (MAS) for the development of high-yielding U.S. Western Shipping market types with superior fruit quality.

## Materials and methods

A set of 81 recombinant inbred lines (RIL;  $F_7$ ) was developed from a cross between U.S. Department of Agriculture line USDA-846-1 ( $P_1$ ) and 'Top Mark' ( $P_2$ ) (Zalapa 2005; Zalapa et al. 2007). 'Top Mark' is andromonoecious, possesses between two to four lateral branches, and produces a diffuse, distal fruit

setting habit typical of vining melon types. The early flowering, monoecious line USDA-846-1 possesses a fractal growth habit (5–8 primary lateral branches), and bears fruit at the base of the plant (Zalapa 2005; Zalapa et al. 2007). This line, which is characterized by its highly branched (fractal growth habit) originated from crosses between an exotic accession from Costa Rica [CR-1; *C. melo* ssp. *agrestis* (Naud.) Pangalo] and a F<sub>1</sub> hybrid plant derived from a cross between USDA line FMR#8 (derived from Middle Eastern melons) × line SC#6 (derived from U.S. Eastern market type melons). Detailed origin and/or pedigree information and descriptions of both CR-1 and USDA-846-1 are available in Zalapa (2005) and Zalapa et al. (2007).

The RIL population, parental lines and their F<sub>1</sub> and F<sub>2</sub> progeny, and three commercial cultivars (“Esteem”, “Sol Dorado”, and “Sol Real”; Syngenta Seeds, Gilroy, CA) were planted and evaluated at the University of California Desert Research and Extension Center in El Centro, CA and the University of Wisconsin Experimental Farm in Hancock, WI during the spring and summer of 2004, respectively. In Wisconsin, seeds were sown (Growing Mix No. 2; Conrad Fafard, Inc., Agawam, MA) in a greenhouse (Madison, WI), and seedlings were transplanted at the three-leaf stage every 0.35 m within rows on 2 m centers (72,600 plants/ha) into Planefield loamy sand (Typic Udipsamment) soil. In California, seeds were sown directly into Imperial silty clay Vertic Torrifluvents soil at the same row and plant spacing as that used in Wisconsin. Plants were arranged in a randomized complete block design consisting of four blocks with 10 plants per treatment plot in both locations. “Esteem”, “Sol Dorado”, and “Sol Real” were used as controls to provide a benchmark for fruit maturation rate comparisons. F<sub>1</sub> and F<sub>2</sub> progeny were included in the analysis for comparative purposes with the parental lines and RIL populations to provide a measure of dominance effects since in inbred populations, the additive variance is expected to be higher than the dominance variance, and thus in this population the importance of dominance variance may be underestimated.

### Data collection

Five mature fruit in Wisconsin and seven in California within treatment plots were evaluated for soluble solids

content (SSC), mesocarp pressure (MP), fruit diameter (FD) (mesocarp + exocarp; FD), seed cavity diameter (endocarp; SCD), seed cavity to FD ratio (C:D), FS, and percentage of exocarp netting (PN) at time of harvest. Preliminary studies conducted during 2003 in CA and WI indicated that examination of fruit at full-slip maturity in transverse section at the blossom- and stem-end provided the most precise estimation of MP and SSC (Paris et al. 2003). Data of SSC, MP, FD, SCD, and C:D were categorized as quantitative data. Fruit samples (~3 cm<sup>3</sup>) for SSC (i.e., BRIX in % ± 0.1) were analyzed using a digital BRIX refractometer (Model DR103L, QA Supplies, Norfolk, VA), and MP was measured as pressure to compress (kg/cm) tissue sampled ~2 cm below the exocarp using a pentrometer employing a 0.79 cm tip (Model# FT 011, Effigy, Alfonsine, Italy). Fruit diameter was measured using a standard ruler (mm), measuring the diameter of the melon fruit from rind to rind. Similarly, SCD was measured (mm) as the diameter of the cavity in which the seeds are housed. The ratio of seed cavity and FD was calculated using the previously mentioned data points. Data of FS and PN were categorized as non-metric data. Fruit shape was classified by visual inspection as round, round-flattened, oblate [spheroid; length: diameter ratio (L:D) > 1.5], oblong (blossom-end larger than stem-end; L:D 1.5–2), pyriform (having a secondary constriction; L:D 1.5–2), elliptical (blossom- and stem-end equal size; L:D 2–3), and elongate (L:D > 3). Thus, fruits were assigned values on a continuous scale from round (1) to elongate (7). A single value for PN was assigned per plot based on the visual inspection of at least 10 mature fruit of the same size.

### Statistical analysis

Variance components were estimated employing restricted maximum likelihood (REML), and each variance estimate was tested for significance using the likelihood ratio statistic (Littell et al. 1996). The linear random effects model for such ANOVA was the following:  $Y = \mu + L + B(L) + F + L \times F + e$ ; where Y is the trait,  $\mu$  is the common effect, L is the location effect, B(L) is the block within location effect, F is the effect of the RIL, L × F is the location × RIL interaction, and e is the plot to plot variation within RIL. The parental lines and

commercial varieties were considered fixed effects. The phenotypic distributions for each trait in the RIL were evaluated for normality by box plot analyses.

Best linear unbiased predictors (BLUPs; Bernardo 1996), standard errors (S.E.), 95% confidence intervals (C.I.s) were estimated for each RIL family using the *solution* option of the *random* statement of the *proc mixed covtest* procedure in SAS (SAS Institute 1999). Best linear unbiased estimators (BLUEs) were also estimated for P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, and commercial varieties using the *solution* option of the *model* statement of the *proc mixed covtest* procedure. This procedure estimates the values of fixed effects from the raw data while making variable value adjustments during fixed effects estimations (de Leon et al. 2005). When the BLUE of the parental and/or commercial varieties were outside the C.I.s of the BLUP for the RILs, such genotypes were considered to be significantly ( $P \leq 0.05$ ) different from each other.

In order to assess whether  $G \times E$  interactions were due to trait magnitude changes between locations or changes in the direction of the response (i.e., RIL rank changes), Spearman (rank) correlation coefficients ( $r_s$ ) were calculated using RIL data for each individual trait across locations according to Yan and Rajcan (2003). When the correlation coefficient between data across locations was  $r_s \leq 0.4$ ,  $G \times E$  interactions were considered more likely to be due to RIL rank changes, and when  $r_s \geq 0.4$ ,  $G \times E$  interactions were considered more likely to be due to trait magnitude changes between locations. Also, in order to evaluate the reliability of RIL performance across traits and locations, the percentage of RIL performance concordance for each trait across locations was calculated for the top 20 performing families (i.e., % RIL that matched in top 20 in both locations).

Phenotypic correlations ( $r$ ;  $n = 81$ ) between pairs of traits were calculated by location using the *proc corr spearman* procedure of SAS Institute (1999).

The broad-sense heritabilities based on RIL BLUPs ( $h_{BF}^2$ ) were calculated as  $h_{BF}^2 = (\sigma_F^2)/\sigma_{PF}^2$ ; where  $\sigma_F^2$  and  $\sigma_{PF}^2$  are the variance among RIL and phenotypic variance based on RIL BLUPs, respectively. The estimate of  $\sigma_{PF}^2$  was calculated as  $\sigma_F^2 + \sigma_{L \times F}^2/B + \sigma_E^2/BL$ ; where B, L,  $\sigma_F^2$ ,  $\sigma_{L \times F}^2$  and  $\sigma_E^2$  refer to the number of blocks, the number of locations, the variance among RIL, the variance due to location  $\times$  RIL interactions, and the plot-to-plot

variation within RIL, respectively (Falconer and Mackay 1996). The standard error of broad-sense heritabilities based on RIL BLUPs were calculated as  $S.E.(h_{BF}^2) = [\text{Var}(\sigma_F^2)]^{1/2}/\sigma_{PF}^2$ .

## QTL Mapping

QTL were positioned on a 190-point genetic map previously described by Zalapa et al. 2007. This map possesses 15 linkage groups spanning 1,116 cM with a mean marker interval of 5.9 cM. Markers were assigned to linkage groups using LOD values thresholds of 5.0 (173 markers) and 3.0 (16 markers and the *a* locus) and recombination frequency of 0.35. Windows QTL Cartographer 2.0 (Wang et al. 2001–2004) was used to identify QTL by composite interval mapping (Zeng 1994). Each of the seven traits analyzed was treated individually by location, and minimum LOD (average = 3.1) threshold values were calculated independently by using 1000 permutation (Churchill and Doerge 1994). A stepwise forward regression procedure employing a walking speed of 1 cM, a window size of 5 cM, and the inclusion of up to 15 maximum background marker loci was used to eliminate background effects inherent among linked multiple QTL. QTL positions are reported herein using the nearest marker, and when the positions of QTL affecting a trait overlapped among locations, they were interpreted to be the same QTL if they fell within a distance of 10 cM. Additive (a) effects and phenotypic variance explained by QTL ( $R^2$ ) were estimated at the highest peaks depicted by QTL Cartographer analyses. Positive additive QTL effects were interpreted as effects produced by alleles contributed by USDA 846-1.

## Results

### Analysis of variance

The likelihood ratio tests of the variance component analyses indicated the existence of significant differences ( $P \leq 0.05$ ) among RIL for all traits (Table 1). Although, the location effect was not significant for any trait, the combined analyses revealed significant ( $P \leq 0.001$ ) environment  $\times$  genotypes interaction effects for all of the traits examined. Spearman correlations ( $r_s$ ), between

**Table 1** Estimates of variance components, broad-sense heritabilities, and Spearman correlation (rank) coefficients ( $r_s$ ) for fruit quality traits based on 81 melon (*Cucumis melo* L.)recombinant inbred lines derived from a cross of USDA 846-1 ( $P_1$ ) × ‘Top Mark’ ( $P_2$ ) grown at El Centro, Calif. and Hancock, Wisc. in 2004

Source of variation	Soluble solids content (SSC)		Mesocarp pressure (MP)		Fruit diameter (FD)	
	Variance component	Percent of total <sup>a</sup>	Variance component	Percent of total	Variance component	Percent of total
Location [L]	0.47 ± 0.69 n.s. <sup>b</sup>	12.3	0.06 ± 0.096 n.s.	4.4	0.93 ± 1.32 n.s.	31.1
Block (Location) [B(L)]	0.03 ± 0.02 n.s.	0.7	0.003 ± 0.003 n.s.	0.2	0.01 ± 0.01 n.s.	0.2
Family [F]	0.84 ± 0.23**	22.0	0.28 ± 0.077**	19.5	0.98 ± 0.18**	32.8
Family × Location [F × L]	0.98 ± 0.16**	25.8	0.33 ± 0.057**	23.5	0.27 ± 0.05**	9.0
Family × Block (Location) [F × B(L)]	1.50 ± 0.03	39.2	0.74 ± 0.014	52.3	0.80 ± 0.02	26.9
Total		100.0		100.0		100.0
$h^2_{BF}$	0.66 ± 0.14		0.61 ± 0.08		0.85 ± 0.12	
( $r_s$ )	0.44**		0.43**		0.03 n.s.	
Top 20 RIL concordance (%) <sup>c</sup>	50		60		20	

Source of variation	Seed cavity diameter (SCD)		Cavity:Diameter (C:D)	
	Variance component	Percent of total	Variance component	Percent of total
Location [L]	0	0	0.141 ± 0.203 n.s.	37.2
Block (Location) [B(L)]	0.007 ± 0.004**	1.3	0.006 ± 0.004 n.s.	1.7
Family [F]	0.214 ± 0.039**	39.6	0.067 ± 0.013**	17.7
Family × Location [F × L]	0.051 ± 0.010**	9.4	0.022 ± 0.005**	5.7
Family × Block (Location) [F × B(L)]	0.268 ± 0.007	49.7	0.144 ± 0.004	37.8
Total		100.0		100.0
$h^2_{BF}$	0.82 ± 0.05		0.74 ± 0.1	
( $r_s$ )	0.76**		0.14 n.s.	
Top 20 RIL concordance (%)	70		20	

<sup>a</sup> Percent of variance component contribution to the total variance<sup>b</sup> \*, \*\*, n.s. indicates that the effect is significant at  $P \leq 0.05$ ,  $P \leq 0.01$ , and not significant, respectively<sup>c</sup> Top 20 RIL (%) = RIL performance concordance (i.e., % RIL that matched in top 20 in both locations)

environments indicated that the interactions between family and environment for the traits examined were due to both magnitude ( $r_s = 0.76$ , SCD) and rank location changes among ( $r_s = 0.44$ , SSC; 0.43, MP; 0.03, FD; and 0.14, C:D) among the RIL. Given genotype × location interactions effects detected for all traits, data are hereafter presented by location (Tables 2 and 3). Despite significant location × family interactions for SSC, MP, and SCD, relatively high trait performance concordance values for the top 20 highest performing families (50, 60 and 70%, respectively; Table 1) and rank correlations (0.44, 0.43, and 0.76, respectively; Table 1) between environments indicate that these traits should allow consistent estimation of genetic parameters.

### Mean comparisons

Fruit quality characteristics of the USDA 846-1 ( $P_1$ ), “Top Mark” ( $P_2$ ), “Esteem” (ES), “Sol Dorado” (SD), and “Sol Real” (SR) varied dramatically (Table 2). Likewise, the RIL examined were phenotypically diverse in fruit quality characteristics that were normally distributed.

### Parents and commercial varieties

Mean BLUE values of  $P_1$  for SSC (12.7), SCD (5.2), and C:D (0.5) were larger in WI than in CA (Table 2). In contrast, mean BLUE values for  $P_2$  for SSC (9.5), FD (9.7), and SCD (4.7) were lower in WI than in CA. The MP and C:D of both parents were

**Table 2** Best linear unbiased estimations (BLUEs) of USDA 846-1 ( $P_1$ ), “Top Mark” ( $P_2$ ), “Esteem” (ES), “Sol Real” (SR), “Sol Dorado” (SD),  $F_1$ , and  $F_2$ , and best linear unbiased predictions (BLUPs) of a melon (*Cucumis melo* L.) RIL

population, their standard errors (S.E.), and confidence intervals (C.I.) for yield components of plants grown at El Centro, Calif. and Hancock, Wisc. in 2004

Wisconsin	BLUE							BLUP	C.I. (95 %)	
	$P_1$	$P_2$	ES	SR	SD	$F_1$	$F_2$		Lower	Upper
SSC	12.65*	9.54*	7.92*	8.63*	9.50*	10.65 n.s.	12.38*	10.23 ± 0.18	9.65	10.82
MP	1.93*	2.08*	2.37 n.s.	2.7 n.s.	1.94*	2.77*	2.25 n.s.	2.43 ± 0.23	2.10	2.76
FD	11.47*	9.74*	11.38*	11.23*	10.51 n.s.	11.45*	11.00 n.s.	10.61 ± 0.12	10.23	11.00
SCD	5.20*	4.66*	5.12 n.s.	4.99 n.s.	4.71 n.s.	5.47*	4.99 n.s.	4.93 ± 0.73	4.70	5.17
C:D	0.45 n.s.	0.48 n.s.	0.45 n.s.	0.44 n.s.	0.45 n.s.	0.48 n.s.	0.45 n.s.	0.47 ± 0.01	0.44	0.48
California	BLUE							BLUP	C.I. (95%)	
	$P_1$	$P_2$	ES	SR	SD	$F_1$	$F_2$		Lower	Upper
SSC <sup>a</sup>	12.00*	11.37 n.s.	10.18*	11.83 n.s.	10.65 n.s.	12.05*	12.28*	11.17 ± 0.167	10.45	11.89
MP <sup>b</sup>	2.55 n.s.	2.47*	1.41*	2.52 n.s.	1.29*	2.48*	3.13 n.s.	2.84 ± 0.081	2.49	3.19
FD <sup>c</sup>	12.26 n.s.	12.51 n.s.	12.37 n.s.	14.05*	13.41*	12.34 n.s.	11.67 n.s.	11.93 ± 0.154	11.27	12.59
SCD <sup>d</sup>	4.74 n.s.	5.20 n.s.	4.69 n.s.	5.25 n.s.	4.64 n.s.	4.79 n.s.	4.92 n.s.	4.92 ± 0.083	4.56	5.28
C:D <sup>e</sup>	0.39*	0.42 n.s.	0.38*	0.37*	0.35*	0.39*	0.42 n.s.	0.42 ± 0.004	0.40	0.43

<sup>a</sup> SSC = Melon fruit from each entry were analyzed for total sugar

<sup>b</sup> MP = Punch test at stem end and blossom end using a penetrometer with a 0.79 cm tip

<sup>c</sup> FD = Melon fruit cut horizontally for fruit diameter measurement

<sup>d</sup> SCD = Seed cavity diameter measured at the center-most portion of horizontally sectioned fruit

<sup>e</sup> C:D = Ratio of fruit diameter and seed cavity calculated as SCD:FD

\*, n.s. = the BLUEs of a parental line ( $P_1$  and  $P_2$ ), their hybrid, and/or “Esteem”, “Sol Real”, and “Sol Dorado” considered significantly different ( $P \leq 0.005$ ) from the average of the RIL when values were outside the C.I. limit of the RIL population BLUPs; the BLUEs of the parental line, their hybrid, and/or “Esteem”, “Sol Real”, and “Sol Dorado”

larger and smaller in CA than in WI, but the FD of both parents were smaller in WI than in CA.

The SSC BLUE values of  $P_1$  were higher than that of  $P_2$  and the commercial varieties at both locations. Although fruit mesocarp of  $P_2$  (2.1) was firmer than  $P_1$  (1.9) and ‘Sol Dorado’ (1.9) in WI, it was not as firm as ‘Esteem’ (2.4) and ‘Sol Real’ (2.7) at that location. In contrast, the firmness of  $P_1$  (2.6),  $P_2$  (2.5), and ‘Sol Real’ (2.5) fruit were similar in CA, but firmer than ‘Esteem’ (1.4) and ‘Sol Dorado’ (1.3). Although the fruit of  $P_1$  were slightly smaller (FD = 12.3) than  $P_2$  (12.5) in CA, they were comparatively smaller in size than ‘Sol Real’ (14.1) and ‘Sol Dorado’ (13.4). In contrast, fruit of  $P_2$  (9.7) and the three controls were smaller than  $P_1$  (11.5) in WI. Similarly, fruit cavity size differed between  $P_1$  [5.2 cm (WI), 4.7 cm (CA)] and  $P_2$  [4.7 cm (WI), 5.2 cm (CA)] depending on growing location, where the cavity size of  $P_1$  was larger than  $P_2$  and all

commercial varieties in WI, but  $P_1$  was similar and  $P_2$  was larger in size than commercial varieties in CA. The C:D of  $P_1$  was lower than  $P_2$  in each location, but both parents were larger than commercial varieties regardless of growing location.

#### Parents, $F_1$ , $F_2$ , and RIL

There were many interesting comparisons to be made using the BLUP and BLUE values of the parental lines and their progeny; however, only a few of the most interesting are highlighted next. For all traits at least one parent was significantly ( $P \leq 0.05$ ) different than the average of the RIL population (BLUE vs. BLUP C.I. comparisons), except for SCD in CA and C:D in WI, indicating that the parental performance deviated from the population average (BLUP value; Table 2). However, individual RIL (Data not presented) were observed that transgressed the

performance of either parent and that of  $F_1$  and  $F_2$  progenies for all traits examined. The collective RIL BLUP value for SSC and FD were, on average, smaller than the BLUE of  $P_1$  and  $P_2$  at both locations. Similarly, the SSC and FD BLUE values of the  $F_1$  and  $F_2$  progeny were higher than the RIL average and similar or higher than the parental lines in both locations. Although, the RIL BLUP values of MP were higher than the parental lines BLUE values, at least one of the  $F_1$  and/or  $F_2$  progenies possessed higher MP values than the RIL average. Similarly, mean BLUE values of the  $F_1$  and/or  $F_2$  progenies for MP matched or exceeded, on average, the parental lines at both locations. The high-parent and/or mid-parent heterosis (i.e., transgressive segregants; Table 2) observed for some traits (e.g., SSC, FD, and MP) and the overall decrease on mean performance of the RIL indicates at some dominance effects for these traits, which is in agreement with the oligogenic inheritance of economically traits in melon (Zalapa et al. 2006).

#### Phenotypic correlations

Although most correlations between traits were not consistent across environments, significant correlations are reported herein as a precedent for other genetic studies involving fruit quality traits as recommended by Lippert and Hall (1982). Significant ( $P \leq 0.05$ ) phenotypic correlations ( $r$ ;  $n = 81$ ) were detected between fruit quality components. For example, MP was negatively correlated with SSC ( $r = -0.24$ , WI) and positively correlated with PN ( $r = 0.24$ , WI). Fruit diameter was positively correlated with SCD ( $r = 0.76$ , WI) and negatively correlated with FS ( $r = -0.39$ , WI). Seed cavity diameter was negatively correlated with MP ( $r = -0.34$ , CA) and FS ( $r = -0.53$ , WI), while being positively correlated to C:D ( $r = 0.33$ , CA). The seed cavity to FD ratio (C:D) was negatively correlated to MP ( $-0.22$ , CA) and positively correlated with SCD ( $0.38$ , CA) and PN ( $0.24$ , CA).

#### Heritability estimates

Broad-sense heritabilities calculated using CA and WI data were 0.66 for SSC, 0.61 for MP, 0.85 for FD, 0.82 for SCD, and 0.74 for C:D, respectively (Table 1).

#### QTL mapping

Fifty-seven QTL were detected for seven traits at two locations [SSC = 10, MP = 8, FD = 6, SCD = 9, C:D = 8, FS = 10, and PN = 6, (LOD 2.7–13.6); Table 3]. These QTL were distributed across 12 linkage groups. Twelve of such QTL were detected in the two locations tested. Two QTL were consistently detected for SSC (*ssc7.4* and *ssc10.8*), three for MP (*mp7.2*, *mp10.3*, and *mplg7.5*), three for SCD (*scd1.1*, *scd5.4*, and *scd8.5*), one for C:D (*cd2.1*), one for PN (*pn2.1*) and two detected for FS (*fs1.1* and *fs2.3*). Thirteen (21%) QTL were detected consistently across locations. Therefore, a total of 45 unique QTL were detected between the two locations, such that five QTL were localized in linkage group I, eight in II, two in V, five in VI, six in VII, seven in VIII, two in IX, three in X, four in XI, one in XII, one in LG7, and one in LG9 (Fig. 1). The proportion of the phenotypic variance explained by single QTL ( $R^2$ ) ranged from 4% (*fs1.2*) to 29% (*fs2.3*). Major QTL ( $R^2 \geq 20\%$ ) were detected for MP (*mp7.2*), FD (*fd11.6*), SCD (*scd8.5*), and two for FS (*fs2.3*). Both parental lines contributed horticulturally desirable alleles depending on the traits examined. USDA-846 contributed most alleles associated with improved soluble solids (*ssc7.4*, *ssc8.5*, *ssc8.6*, *ssc9.7*, and *ssc10.8*) and netting (*pn2.1*, *pn5.2*, *pn8.4*, and *pn11.5*), but larger seed cavity to FD ratio (*cd7.2*, *cd8.5*, and *cd10.7*) and SCD (*scd1.1* and *scd5.4*).

#### Discussion

Effective and efficient deployment of molecular markers in MAS requires a relatively well saturated map where tight linkages exist between markers and target traits. A saturated melon genetic map is predicted to have a total length of between 1,500 and 2,000 cM distributed across 12 linkage groups (Baudracco-Arnas and Pitrat 1996). However, most published melon maps describe more linkage groups than the basic chromosome number for this species, and therefore do not completely define the genome (Baudracco-Arnas and Pitrat, 1996; Wang et al. 1997; Liou et al. 1998; Danin-Poleg et al. 2002; Silberstein et al. 2003). A map developed by Zalapa et al. (2007) in a Group *Cantalupensis* background was used herein as the backbone for characterizing

**Table 3** Linkage group positions (cM) of QTL along with their associated logarithm of odds (LOD), percentage of phenotypic variation ( $R^2$ ), and additive effect for yield components in a recombinant inbred line (RIL) population

derived from a cross between melon (*Cucumis melo* L.) lines USDA 846-1 and “Top Mark” evaluated in Hancock, Wisc. and El Centro, Calif. in 2004

Trait <sup>a</sup>	Linkage group	QTL <sup>b</sup>	Trial location	Position (cM)	Nearest marker locus <sup>c</sup>	LOD	$R^2$	Additive effect <sup>d</sup>
SSC	I	<i>ssc1.1</i>	WI	18.91	TJ27	6.0	0.10	−0.48
	II	<i>ssc2.2</i>	CA	12.11	OPAD14-400	5.4	0.10	−0.39
	VI	<i>ssc6.3</i>	WI	111.71	OPAI8-800	8.6	0.18	−0.60
	VII	<i>ssc7.4</i>	CA	94.11	E19M51-302	3.9	0.08	0.31
	VII	<i>ssc7.4</i>	WI	103.91	E24M48-133	3.4	0.05	0.31
	VIII	<i>ssc8.5</i>	CA	13.8	OPAY1-831	8.7	0.18	0.50
	VIII	<i>ssc8.6</i>	WI	50.41	OPAY16-400	4.4	0.07	0.46
	IX	<i>ssc9.7</i>	WI	3.01	CMATN22	3.7	0.08	0.39
	X	<i>ssc10.8</i>	CA	9.41	DoCMCTT144-100	5.6	0.17	0.43
	X	<i>ssc10.8</i>	WI	14.31	CMGA172	6.6	0.11	0.49
MP	VI	<i>mp6.1</i>	WI	138.41	E19M47-329	5.5	0.14	−0.64
	VII	<i>mp7.2</i>	CA	42.11	E19M54-248	6.5	0.20	−0.30
	VII	<i>mp7.2</i>	WI	43.51	E18M62-100	3.3	0.08	−0.51
	X	<i>mp10.3</i>	WI	16.91	E26M48-265	3.6	0.09	−0.51
	X	<i>mp10.3</i>	CA	20.91	E26M48-265	3.2	0.10	−0.19
	XII	<i>mp12.4</i>	WI	68.21	OPAC11-1350	4.7	0.12	0.60
	LG7	<i>mplg7.5</i>	CA	0.01	OPG8-400	3.1	0.07	−0.17
	LG7	<i>mplg7.5</i>	WI	4.01	OPG8-400	3.4	0.12	−0.67
FD	I	<i>fd1.1</i>	WI	71.61	CMCT505	3.3	0.06	0.24
	II	<i>fd2.2</i>	WI	24.31	OPAI9-250	5.2	0.10	−0.30
	II	<i>fd2.3</i>	CA	78.81	E14M50-159	3.8	0.13	−0.45
	VI	<i>fd6.4</i>	CA	35.31	OPR5-500	4.4	0.15	−0.78
	VIII	<i>fd8.5</i>	WI	56.51	OPAE3-600	7.8	0.15	−0.38
	XI	<i>fd11.6</i>	CA	43.31	OPAI8-250	7.8	0.28	−0.85
SCD	I	<i>scd1.1</i>	WI	67.61	CMCT505	3.5	0.08	0.12
	I	<i>scd1.1</i>	CA	67.61	CMCT505	5.7	0.16	0.22
	II	<i>scd2.2</i>	WI	24.81	CMGT108	6.6	0.16	−0.18
	II	<i>scd2.3</i>	CA	43.01	OPAL8-400	3.5	0.09	−0.17
	V	<i>scd5.4</i>	CA	43.11	CMTCN9	4.9	0.13	0.19
	V	<i>scd5.4</i>	WI	45.11	CMTCN9	3.1	0.07	0.11
SCD	VIII	<i>scd8.5</i>	CA	44.81	CMATTN29	7.8	0.24	−0.28
	VIII	<i>scd8.5</i>	WI	45.61	CMATTN29	7.3	0.17	−0.18
	VIII	<i>scd8.6</i>	WI	154.31	DoCMTTAN28-170	3.9	0.09	−0.13
C:D	II	<i>cd2.1</i>	CA	80.81	E14M50-159	2.7	0.07	−0.01
	II	<i>cd2.1</i>	WI	80.81	E14M50-159	5.4	0.17	−0.01
	VII	<i>cd7.2</i>	CA	0.01	CMGAN48	4.7	0.13	0.01
	VII	<i>cd7.3</i>	CA	78.21	CMGAN21	4.3	0.13	−0.01
	VII	<i>cd7.4</i>	WI	103.91	E24M48-133	3.6	0.10	−0.01
	VIII	<i>cd8.5</i>	CA	55.71	OPI11-500	3.0	0.08	0.01
	IX	<i>cd9.6</i>	CA	4.01	CMATN22	3.6	0.12	−0.01
	X	<i>cd10.7</i>	WI	0.01	OPW16-800	4.2	0.12	0.01

**Table 3** continued

Trait <sup>a</sup>	Linkage group	QTL <sup>b</sup>	Trial location	Position (cM)	Nearest marker locus <sup>c</sup>	LOD	R <sup>2</sup>	Additive effect <sup>d</sup>
PN	II	<i>pn2.1</i>	WI	16.31	OPAI9-250	3.2	0.10	3.04
	II	<i>pn2.1</i>	CA	20.31	OPAI9-250	4.0	0.14	6.18
	V	<i>pn5.2</i>	WI	44.11	CMTCN9	5.3	0.18	5.62
	VI	<i>pn6.3</i>	CA	160.91	OPO6-1375	5.0	0.17	−12.43
	VIII	<i>pn8.4</i>	CA	169.31	OPAH14-831	5.0	0.17	5.76
	XI	<i>pn11.5</i>	WI	36.31	CMGA104	4.5	0.15	3.54
FS	I	<i>fs1.1</i>	WI	51.41	OPAL11-1250	3.8	0.05	−0.66
	I	<i>fs1.1</i>	CA	52.01	OPAL11-950	4.2	0.10	−0.64
	I	<i>fs1.2</i>	WI	64.31	OPP12-564	3.1	0.04	0.56
	II	<i>fs2.3</i>	CA	73.81	E14M50-159	6.6	0.26	0.86
	II	<i>fs2.3</i>	WI	80.81	E14M50-159	13.6	0.29	0.96
	VI	<i>fs6.4</i>	CA	37.31	OPR5-500	3.2	0.09	−0.49
	VII	<i>fs7.5</i>	CA	51.51	OPAD15-830	3.3	0.08	−0.51
	XI	<i>fs11.6</i>	CA	0.01	OPAO7-600	4.7	0.12	−0.54
	XI	<i>fs11.7</i>	WI	61.51	TJ23	4.3	0.07	0.49
	LG9	<i>fslg9.8</i>	WI	32.61	E25M17-165	6.2	0.10	0.61

<sup>a</sup> Abbreviation of trait name where SSC = soluble solids content; MP = mesocarp pressure; FD = fruit diameter; SCD = seed cell diameter; C:D = SCD:FD ratio; FS = fruit shape and; PN = percent netting at full-slip; <sup>b</sup> QTL designated by abbreviated trait name, linkage group number, and QTL number; <sup>c</sup> Marker locus closest to the QTL effect; <sup>d</sup> Additive effect as obtained from a composite interval mapping (CIM) model resident in QTL cartographer (Wang et al. 2001–2004). The molecular map is according to Zalapa et al. (2007) and linkage groups follow the nomenclature by Perin et al. (2002c)

QTL associated with fruit quality components. Even though the marker interval in this map is relatively small (5.9 cM), this map must be considered relatively unsaturated since it consists of 15 linkage groups, and only spans between 50 to 66% of the predicted genome length. Nevertheless, the genetic analysis conducted herein identified QTL that not only confirmed several marker-trait associations (FS = 7, SSC = 6, C:D = 3, SCD = 1, and PN = 1; Fig. 1) detected by Perin et al. (2002a) and Monforte et al. (2004), Eduardo et al. (2007), and Obando et al. (2008) in a Group Inodorus mapping population, but also provided more definitive confidence intervals for these QTL. Furthermore, additional, unique marker-fruit quality trait associations were defined which could be used for MAS in populations derived from the Zalapa et al. (2007) mapping population.

Environmental effects on trait expression and RIL performance

Yield component QTL in melon are dramatically affected by growing environment and their

expression is influenced by complex epistatic interactions (Zalapa 2005; Zalapa et al. 2006, 2007). Although several fruit quality traits (e.g., flesh color, rind sutures, spots on rind, and some taste attributes) are simply inherited (Perin et al. 1999), traits such as fruit weight, sugar content, external and internal flesh color are metric with complex inheritances (Monforte et al. 2004). There were important performance differences among genotypes that were location dependent (Table 1 and 2). Such location differences in rank and magnitude among RIL are likely due, in large part, to temperature, relative humidity (RH), and rain index differences between locations (i.e., CA spring and WI summer) (Table 2). While the average temperature, RH, and precipitation in CA during the growing season was 24.4°C (33.6–14.8°C), 41%, and 0.51 cm/month, respectively, the mean values for these environmental parameters in WI were 18.9°C (24.3–13.1°C), 75%, and 9.40 cm/month, respectively. It is likely that the near optimal (i.e., rapid growing) conditions in contributed dramatically to plant vegetative growth where plants in California grew more rapidly (~2 times) and larger (~1 m vs. ~3 m in diameter) than plants in Wisconsin (by

visual inspection), thus allowing, for example, the accumulation of higher SSC and larger FD in California than in Wisconsin. Such growth-related differences in melon have been reported previously for other traits (e.g., SSC; Monforte et al. 2004; Eduardo et al. 2007; Zalapa et al. 2007).

There were, in fact, important location effects reported herein (e.g., for MP and SCD), but RIL performance rankings (i.e., top 20 RIL concordance % > 50%) and environment rank correlations (i.e.,  $r > 0.40$ ) were, in the main, consistent across environments (Tables 1). Thus, differences in SSC, MP, and SCD among RIL between locations were primarily of magnitude and not rank. In contrast, location differences in FD and C:D among RIL were of rank order (i.e., high and low performing RIL were inconsistent). However, despite location effects on these traits, nine environmentally independent QTL were detected in the two locations tested [SSC (*ssc7.4* and *ssc10.8*), MP (*mp7.2*, *mp10.3*, and *mplg7.5*), SCD (*scd1.1*, *scd5.4*, and *scd8.5*), C:D (*cd2.1*)]; most of which corresponded to the consistent traits across environments (i.e., SSC, MP, and SCD) where no consistent QTL were identified for FD and only one for C:D.

The development of improved, high yielding melon varieties that bear high quality fruit is difficult. Historically, most of the yield improvement in melon has been due to improved cultural practices, breeding for simply inherited traits (e.g., diseases and pests), and the use of hybrids created from sparingly few elite lines (McCreight et al. 1993). The RIL examined herein were developed from a cross between the U.S. Western Shipping ‘Top Mark’ and USDA-846-1, a unique high yielding fractal line with basal fruit setting (Zalapa 2005; Zalapa et al. 2007). High yielding RIL were identified that produce fruit of varying quality (external and internal). Although most correlations between quality traits were not consistent across environments, significant correlations reported herein could be important for other genetic studies involving fruit quality traits. However, some fruit quality traits are correlated with yield component traits examined in CA and WI (Zalapa et al. 2007). For instance, in this RIL population a significant ( $P \leq 0.01$ ) positive correlation exists between average fruit weight and diameter ( $r = 0.50$ ), but primary branch number and FD are negatively correlated ( $r = -0.37$ ;  $P \leq 0.01$ ), as are

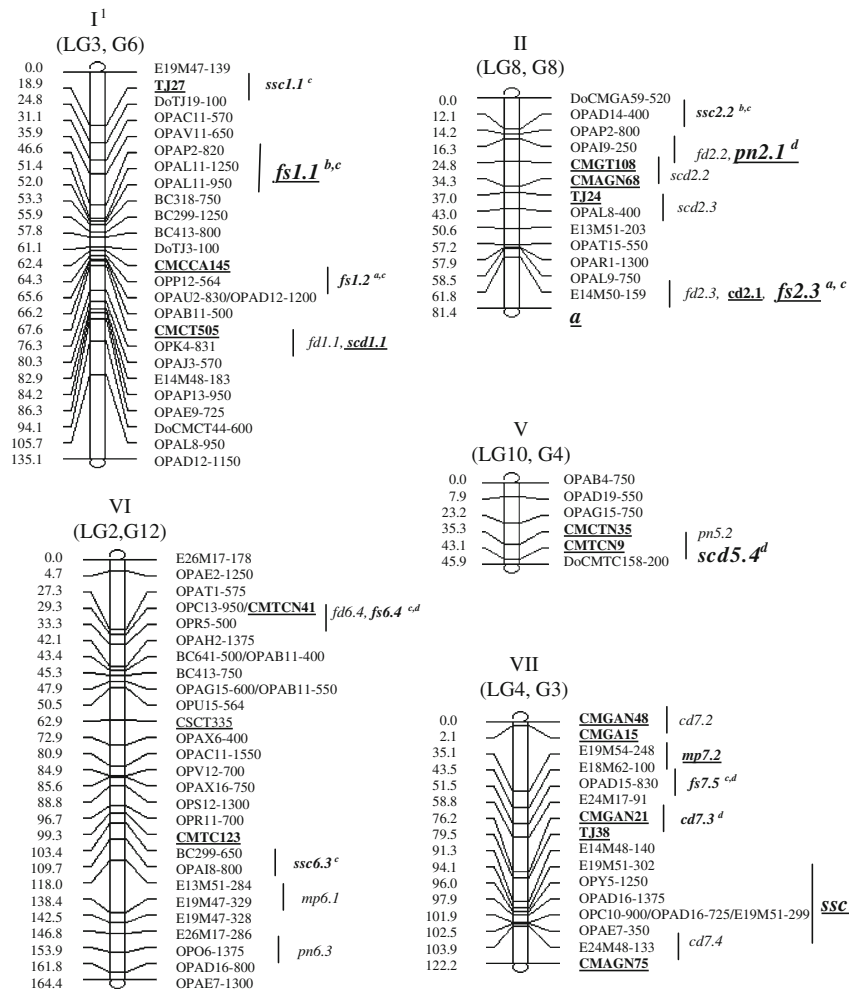
also fruit number and diameter ( $r = -0.50$ ;  $P \leq 0.01$ ). These and other yield and quality phenotypic and linkage associations presented herein and by Zalapa et al. (2007) must be considered when developing MAS strategies.

#### Marker collinearity among melon maps

Recently, Gonzalo et al. (2005) constructed a genetic map (“Songwhan Charmi” × “Pinyonet Piel de Sapo”) consisting of 327 loci (226 RFLPs, 97 SSRs, and 3 SNPs) distributed over 12 linkage groups spanning 1,021 cM. Because SSRs provide common anchor points for syntenic analysis (Katzir et al. 1996; Danin-Poleg et al. 2000, 2002; Perin et al. 2002c), the Gonzalo et al. (2005) genetic map has been proposed as a possible bridge with other melon maps containing common SSR markers. Common SSR anchor markers were used for “cross-identification” of seven of the eleven fruit quality QTL-associated linkage groups identified herein with corresponding groups reported by Gonzalo et al. (2005; Fig. 1, designated by the prefix “G”). Syntenic linkage associations have been documented by Zalapa et al. (2007) on group LG1 (to G1), LG2 (to G12), LG3 (to G6), LG4 (to G3), LG5 (to G9), LG6 (to G11), LG8 (to G8), LG10 (to G4), LG11 and LG13 (to G5), and LG12 (to G7). Moreover, nine linkage groups of Zalapa et al. (2007; LG 1–6, 8, 12, 13) are collinear with those of Perin et al. (2002a, b, c; LG VIII, VI, I, VII, X, XII, II, IX, and XI), which share collinearities with the map of Monforte et al. (2004). Therefore, the molecular map depicted (Fig. 1) is according to Zalapa et al. (2007), but linkage groups follow the current accepted melon nomenclature proposed by Perin et al. (2002c) (I, II, V, VI, VII, VIII, IX, X, XI, and XII and LG7 and LG9 according to Zalapa et al. 2007). The collinearity of these linkage maps is indicative of the syntenic nature of the maps, the affirmative prospects of map merging, and the potential broad application of the QTL-marker associations defined herein.

#### Potential application of QTL for MAS

Several of the fruit quality QTL identified herein were consistent (i.e., location independent) and informative (i.e.,  $\text{LOD} > 3.0$ ;  $R^2 \geq 20\%$ ), and portends their potential utility for MAS (Table 3; Figs. 1



**Fig. 1** Linkage map and locations of quantitative trait loci (QTL) associated with fruit quality components based on 81 melon (*Cucumis melo* L.) recombinant inbred lines (RIL) derived from a cross between USDA 846-1 and “Top Mark.” Footnote 1 represents the molecular map depicted is according to Zalapa et al. (2007) and linkage groups follow the nomenclature by Perin et al. (2002c) (I, II, V, VI, VII, VIII, IX, X, XI, and XII and LG7 and LG9 according to Zalapa et al. 2007). Group numbers in parenthesis (LG1, 2, 3, 4, 5, 6, 8, 10, 11, 12, and 13) and (G1, 3, 4, 5, 6, 7, 8, 9, 11, and 12)

and 2). This assertion is supported by the fact that fruit quality QTL detected herein are collinear with those of the Group Inodorus-based maps of Perin et al. (2002a), Monforte et al. (2004), Eduardo et al. (2007), and/or Obando et al. (2008) (Table 3; Fig. 1). In fact, the map positions of 18 QTL (FS = 7, SSC = 6, C:D = 3, SCD = 1, and PN = 1) were collinear with previous studies in Group Inodorus-based maps. Six of the collinear QTL were detected

correspond to linkage groups in maps the by Zalapa et al. (2007) and Gonzalo et al. (2005), respectively. Underlined markers are common markers between maps. Underlined QTL are environmentally-independent QTL detected herein and <sup>a,b,c,d</sup> correspond to QTL identified in common with Perin et al. (2002a), Monforte et al. (2004), Eduardo et al. 2007, and Obando et al. 2008, respectively. QTL in larger, bold font are environmentally independent and were detected in equivalent regions of at least one of the maps listed above

in both locations in our study (*ssc7.4*, *ssc10.8*, *fs1.1*, *fs2.3*, *pn2.1*, and *scd5.4*). Moreover, at least six of the eight FS QTL detected in our study are likely common to two of the four maps. In fact, linkage I contains a small cluster of FS QTL (*fs1.1* and *fs1.2*) around the same genomic locations (defined by TJ27, CMCCA145, and CMCT505) where FS QTL have been detected by Perin et al. (2002a), Monforte et al. (2004), and Eduardo et al. (2007). In addition, *fs2.3*

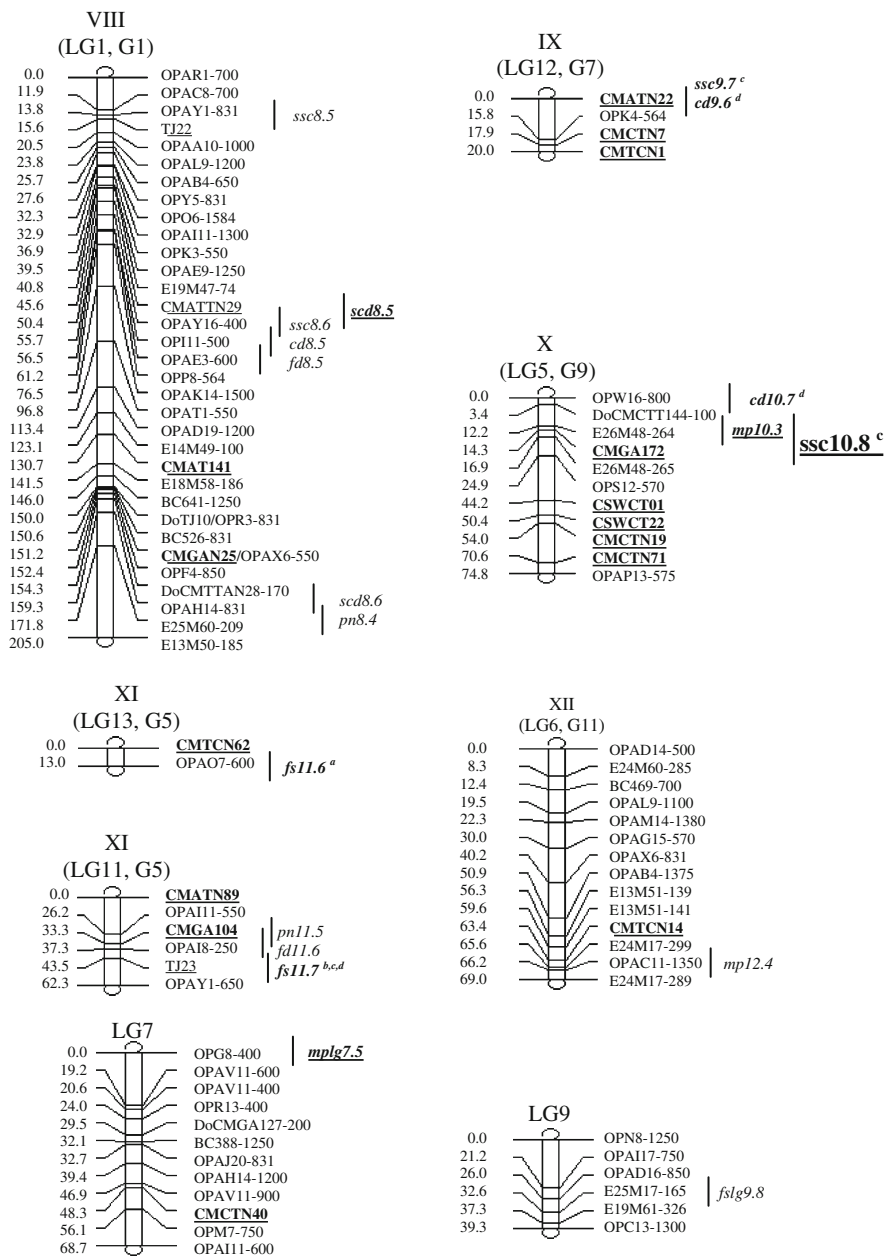
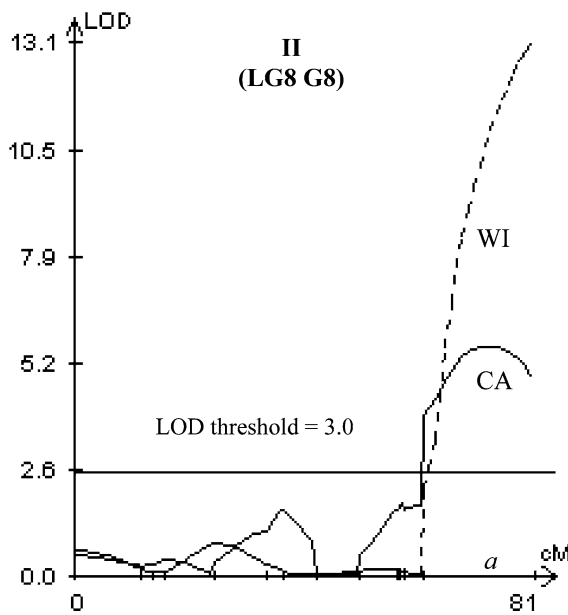


Fig. 1 continued

in our study was also detected by Eduardo et al. (2007) and Perin et al. (2002a) in an equivalent genomic position, around the *a* locus (Perin et al. 2002c). Also, *fs6.4* and *fs7.5* in our study were positioned in equivalent (nearby VI = CMTCN41 and VII = CMGA15 and CMGAN21; Gonzalo et al. 2005) regions of Eduardo et al. (2007) and Obando et al. (2008). Similarly, *fs11.6* and *fs11.7*, reported

herein are located in nearby regions of the Perin et al. (2002a) and Monforte et al. (2004), Eduardo et al. (2007), and Obando et al. (2008), respectively (shared markers, CMATN89, CMTC160, CMGA104, and TJ23; Perin et al. 2002a, b, c; Gonzalo et al. 2005). These collinearities specifically suggest the potential broad applicability of *fs1.1*, *fs1.2*, *fs2.3*, *fs6.4*, *fs7.5*, *fs11.6*, and *fs11.7* for MAS in different



**Fig. 2** A major FS QTL ( $R^2 = 29\%$ ) was detected near the *a* (*andromonoecious*) locus in the RIL population described by Zalapa et al. (2007) using CIM. Mapping of QTL correlated to FS in linkage II also identified significant QTL for FD ( $R^2 = 13\%$ ) and SCD ( $R^2 = 17\%$ ) in this region (not shown)

melon market classes. Finally, soluble solids and other fruit quality QTL were also detected in regions consistent with Monforte et al. (2004), Eduardo et al. (2007), and Obando et al. (2008). For example, the map positions of SSC (*ssc1.1*, *ssc2.2*, *ssc6.3*, *ssc7.4*, *ssc9.7*, and *ssc10.8*), C:D (*cd7.3*, *cd9.6*, and *cd10.7*), PN (*pn2.1*), and SCD (*scd5.4*) were in equivalent regions of Spanish maps.

Not all QTL identified herein and those by other groups are, however, universally applicable for MAS. For example, although SSC QTL (*ssc8.5* and *ssc8.6*; LOD = 8.7 and 4.4,  $R^2 = 18$  and 7%, respectively) were detected in linkage VIII in both our study and the Spanish maps (LG1 versus G1), they are not localized in equivalent map locations. Moreover, although linkage VIII of our map is saturated with several QTL (i.e., SSC, FD, SCD, PN, and C:D), it does not contain QTL for FS (Table 3; Fig. 1) as is the case for the Spanish (Monforte et al. 2004; *fs1.1*) and French maps (Perin et al. 2002a; *fs8.1* and *fs8.2*). Likewise, equivalent QTL were not detected in LGXII (i.e., one shared SSR marker). Finally, QTL associated with the *a* (conditioning *andromonoecious*) locus, need to be further investigated.

Sixty-one percent of the QTL detected for the quality traits studied are located on four linkage groups (i.e., I, II, VII, and VIII, 1, 4,). All four groups include QTL which were location independent (i.e., *scd1.1*, *fs1.1*, *cd2.1*, *fs2.3*, and *pn2.1*, *ssc7.4*, *mp7.2*, and *scd8.5*). Linkage Group II, spanning 81.4 cM, is of specific interest for fruit quality (this study) and yield (Zalapa et al. 2007) traits, since eight QTL potentially valuable have been defined (Table 3; Fig. 1). The *a* (*andromonoecious*) locus is located at the basal region of this linkage group (linkage II; Fig. 1). Three QTL which affect fruit shape (FD = *fd2.3*, SCD = *cd2.1*, and fruit shape = *fs2.3*) were detected near this locus. Likewise, major QTL for average fruit weight and fruit number and weight per plant (II = LG8; *awf8.5*, *fn8.8*, *fw8.12*; LOD = 4.29–14.88,  $R^2 = 0.10 = 0.43$ ) have also been detected near the *a* locus in this RIL population (Zalapa et al. 2007). The location of QTL *fs2.3* (Figs. 1 and 2) is consistent with reported data from Perin et al. (2002a) and Eduardo et al. (2007) and was location independent in our study (California LOD = 6.6 and  $R^2 = 26\%$ ; Wisconsin LOD = 13.6 and  $R^2 = 29\%$ ). Mapping of QTL related to FS in linkage II also identified significant QTL for FD ( $R^2 = 13\%$ ) and SCD ( $R^2 = 17\%$ ) in this region. The performance of FS related traits could be explained by a pleiotropic effect associated with *a* and/or linkage between loci (Falconer and Mackay 1996), and thus additional studies (i.e., fine mapping) will be necessary to determine its effects on fruit development and quality.

An understanding of epistasis is critical to the effective strategic deployment of MAS in plant improvement. Although this population may be considered relatively small (81 lines) for meaningful epistatic analyses, two-dimensional genome analyses conducted in R/qtl (Broman et al. 2003) provided some evidence (i.e., location independent interactions; Data not presented) for the presence of epistatic interactions among genes conditioning fruit the quality traits in melon. Epistatic interactions were detected between linkage VII (around genomic locations defining QTL that control C:D, MP, and FS) and linkage X, near regions associated with C:D, MP, and SSC QTL. Similarly, the region in linkage II associated with the *a* locus apparently interacts with QTL conditioning FS (linkage I), C:D (linkage VII), and PN (linkage II). Although the knowledge of these

interactions and those involved in the expression of melon yield (Zalapa et al. 2007) will be invaluable in designing MAS strategies, further characterization using a larger RIL population will be required to improve the estimation of genetic effects. Their presence herein, however, underscores the premise that effective deployment of the marker-QTL associations for MAS in melon will require careful consideration of prospective marker-trait associations and their interactions as well as fruit maturation physiology (i.e., trait correlations and source/sink relationships) and environmental effects.

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